

## Spatial and temporal use of microhabitats as a key strategy for the colonization of tree bark by *Entomobrya nivalis* L. (Collembola: Entomobryidae)

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### ABSTRACT

Investigations were carried out on the microhabitat utilization of tree bark by *Entomobrya nivalis* (Collembola: Entomobryidae). Population densities of *E. nivalis* were recorded from different microhabitats on the trunks of solitary oak, beech, lime and ash trees in northern Germany. The principal microhabitat types utilized by *E. nivalis* were horizontal and vertical bark crevices, a fruticose (= shrub-like) and a crust-like lichen species. The fruticose lichen species was found to be permanently used, while the crust-like lichen species and the horizontal bark crevices were densely populated under certain climatic conditions. Vertical crevices were particularly heavily used by juveniles. This complementary 'part time use' of microhabitats was explained by food availability as well as by protection from very wet conditions offered by the crust-like lichen and wind- and sun-shelters in crevices. Preferred lichens were often scarce, isolated and small in size, but were still heavily populated.

A mosaic pattern of microhabitats enables *E. nivalis* to colonize bark despite the extreme climatic conditions that occur on exposed tree trunks throughout the year. This permitted: (i) the optimal use of the complete trunk when energetically favourable; (ii) the immigration of middle-aged individuals from adjacent population pools; and (iii) the coexistence of different age-classes. Minute size and eurytopy are considered to be prerequisites for the differentiated, dynamic and flexible use of small-sized microhabitats.

## INTRODUCTION

The edges of the canopy layer are extreme habitats. Abiotically, they are exposed to strong and changeable wind, sun and rain. Underneath the crown such extreme conditions can be found on the exposed upper parts of trunks (Braun, 1992). Moreover, lower trunk regions of isolated trees are also exposed to extreme conditions. This can be recognized by the absence of mosses at heights of only 0.5 m and the impact of wind on neighbouring shrubs and crowns (Nogushi, 1979). Biotically, bark crevices, algae and lichens are often the only microhabitats for arthropods in lower crown-regions and at trunks (at least in temperate latitudes). Each of these cryptogam species can occur as small, isolated patches of some square millimetres or may continuously cover several square metres of bark.

Generally, strategies for arthropods to cope with harsh conditions and patchy resources include: large size, strong sclerotization, shells, ability to dig into the substrate, large-scale wandering or dormancy interrupted by rapid development (Tischler, 1990). Microarthropods like Collembola lack such strategies and are therefore normally restricted to a sheltered, detritivorous life in crevices or below plant cushions (Travé, 1963; Jøger, 1988; Bauer, 1993), except after precipitation (Hale, 1972; T. Bauer, 1979; R. Bauer, 1993).

The exposed and patchy lichens and algae on tree trunks, however, are mainly grazed on by Collembola, oribatid mites and small Psocoptera (Travé, 1963; André, 1975, 1979; Gjelstrup, 1979; Nicolai, 1985, 1986; Büchs, 1988, 1990; Prinzing and Wirtz, 1997, Chapter 23, this volume). None of these organisms is restricted to such extremely exposed, solitary tree trunks (Pschorn-Walcher and Gunhold, 1957; Travé, 1963). These species also occur under more sheltered conditions on the shaded base of tree trunks and in the forest litter-zone (Gisin, 1960; Günther, 1974; Gjelstrup, 1979; Weigmann and Kratz, 1981; Woltemade, 1982; Nicolai, 1985; Büchs, 1988).

How then can such sensitive and eurytopic (occurring in a wide range of habitats) microarthropod species utilize the exposed bark of tree trunks and canopy layers?

Microarthropods might respond to this problem by using *microhabitats* with exceptionally favourable conditions. To test this, information was needed on whether and how: (i) the type of microhabitat (cryptogam species or type of bark crevice) influences densities and phenologies of arthropod species; (ii) microhabitat use interacts with short-term climatic conditions and seasons; and (iii) how the use of the complete tree trunk 'macrohabitat' depends on climate, as reported by Bowden *et al.* (1976) and Bauer (1979).

In general, the spatiotemporal use of the trunk 'macrohabitat' can be restricted to certain ontogenetic stages, since many species need to

transverse the complete trunk-layer in order to reach the food sources or hibernation habitats of the adult stage (Winter, 1972; Schauer mann, 1973; Funke, 1979; Albert, 1982; von Allmen and Zettel, 1982; Nicolai, 1985, 1986; Büchs, 1988, 1990). Also, short-term migrations of Collembola from the surrounding soil lasting for only several hours were observed by Bowden *et al.* (1976) and Bauer (1979). They demonstrated strong increases in Collembola densities on sheltered trunks at night and after rain, by using light-, sticky- and pitfall-traps or by direct observation. Bauer (1979) was also able to enhance this vertical migration in the laboratory by using high air humidities. Under these conditions trunks were a suitable feeding habitat for Collembola and their risk of drowning was lower than in the soil.

Observed vertical and horizontal zonations of microarthropod distribution on tree trunks (Duffey, 1969; Niedballa, 1969; Gjelstrup, 1979; Woltemade, 1982; Nicolai, 1985, 1986; Büchs, 1988; Stubbs, 1989; Braun, 1992; Manhart, 1994) are correlated with climatic conditions. These are accompanied by changes in epiphyte cover, biomass and species composition (Rose, 1974 and authors mentioned above), in moss/lichen zonations (Travé, 1963; Gjelstrup, 1979; Woltemade, 1982; Manhart, 1994) and in lichen growth forms (André, 1979, 1983; Woltemade, 1982). The separate effect of such epiphytes has been demonstrated only twice. André (1979) found that bark covered with thalli of two selected, similar crust-like lichen species differed strongly in their oribatid mite faunas. Also, differentiation of living conditions was found within single thalli of a fruticose lichen species (Prinzing and Wirtz, 1997, Chapter 23, this volume).

No other investigations of the distribution of corticolous microarthropod populations have taken into consideration all common microhabitats and the different microclimatic zones on tree trunks. In this paper such results are presented for *Entomobrya nivalis* L. (Collembola: Entomobryidae), one of the most common Collembola species on trunks in northern Germany. This species often colonizes tree trunks despite its preference for a relative humidity above 80% (von Allmen and Zettel, 1982; André, 1983; Büchs, 1988; Müller-Kraenner, 1990; Prinzing and Wirtz, 1997, Chapter 23, this volume).

## MATERIALS AND METHODS

### Study sites

Research was conducted from August 1993 until April 1994 in five areas near Kiel (northern Germany, hilly landscape, oceanic-temperate climate, less than 50 m above sea level). Additionally, in August and September 1993 an area near Rostock was considered (flat and

climatically more continental, north-east Germany). Trunks of large solitary trees (>2.5 m circumference at a height of 1.5 m) were searched for individuals of *E. nivalis* at heights between 0.8 and 1.8 m. Trees of *Quercus robur* L. (oak), *Fagus sylvatica* L. (beech), *Fraxinus excelsior* L. (ash) and, except in one area, *Tilia* sp. (mainly *T. platyphyllos* Scop.) (lime) were examined. Within each study area, trees were selected in order to minimize distances between the different tree species. Solitary trees are a common feature in these rural areas, mainly along paths and avenues and in meadows. Solitary beech trees mostly grow in small park-like forests or in clearings.

The common types of tree bark microhabitats investigated were:

#### Crevice

1. vertical crevices between bark scales
2. horizontal crevices, always starting at the bark surface inwardly

#### Epiphytes

3. Fruticose lichen species *Evernia prunastri* L.
- 4.-7. Crust-like lichen species *Lepraria incana* L., *Pertusaria albescens* Choisy and Werner, *Lecanora expallens* ACH., *L. conizaeoides* Nyl. ex Crombie,
8. Algae (*Pleurococcus* sp.),
9. Bark surface without epiphytes

Of these, only vertical crevices were absent on beech trunks. In addition, mosses and foliose lichens were found, but they never covered more than 5% of the bark surface – even when only a narrow zone of equal momentary exposures to wind, sun and precipitation was considered. On ash trees the lichens *Buellia punctata* Massal. and *B. griseovirens* Almb. sometimes covered up to 20% of the respective zone of exposure.

From August 1993 to January 1994, 45–50 trees were sampled per month (30% of them at night), in February and March 1994, 28 trees each, and in April, eight trees. Daytime visits started at 08:00 h or, in winter, from dawn and lasted until at least 2 hours before sunset, except when temperatures remained below –5°C (trunks were then sparsely populated). Night visits began at dusk and lasted for 6–9 hours. Different study areas and tree species were sampled in a random order. Nine trees were resampled, but only after a period of at least 3 months.

#### Sampling

Each trunk was divided, by eye, into faces according to their exposure to wind, sun and/or precipitation (= zones covered with a waterfilm) at the moment of investigation. As an example, during windy, sunny weather, mostly four trunk-faces could be differentiated: those exposed

to wind and sun, only to wind, only to sun or to none of them. Each trunk-face was subdivided again according to different momentary exposures within its microrelief (due to positions on bark-ridges and bark-valleys or in front of or behind fruticose thalli). 'Zones of exposure' were defined correspondingly by the combination of exposures of the respective trunk-face and microrelief-zone.

Within each zone, temperature (Gultan Tastootherm D 700), air velocity (thermic anemometer 641 N, Lambrecht Meßgeräte) and air humidity were measured (Valvo-hygrometer, sensor with detached cap and ventilator; after February 1994: Rotronic hygrometer A1), although the Valvo-sensor was mostly too large to measure within the 'valleys' of the bark-relief. All measurements were taken at a height approximately 2 mm above the bark. For each trunk-face five locations were tested for temperature, four for wind and one for air humidity measurements.

*Entomobrya nivalis* densities within different microhabitats were measured by direct counts of individuals with a hand-lens. For each single field of view the trunk was approached with careful movements and viewed from a distance of just 3 cm ( $\times 10$  magnification). In each zone 10 randomly distributed direct counts were made for each microhabitat type present. Thus, individual plots of 18 cm<sup>2</sup> of microhabitat surface were examined.

Inner surface examinations of cavities during the hand-lens-searches were as follows: (a) horizontal crevices were searched in a length that, multiplied by the approximate depth of the crevices, equalled approximately 18 cm<sup>2</sup> (this length was measured in field-of-view diameters); (b) thalli of the fruticose lichen, *Evernia prunastri*, were opened in several layers with a large needle; and (c) vertical crevices were broken up with a knife. The dark cavities of horizontal crevices and thalli of *Evernia prunastri* were illuminated with a small pen-light torch. At night, illumination was necessary for all types of microhabitats and was restricted to a single field of view for less than about 2 seconds at a time. Horizontal crevices were sometimes difficult to survey by eye. They were then additionally examined by scraping with a large needle. Investigation plots of crust-like thalli were completely scraped off on at least one in 10 trunks until mid-September. Later, this was done for all crust-like lichen plots.

Individuals of *Entomobrya nivalis* were mainly determined in the field. Animals were recorded as 'juvenile', 'middle-aged' or 'adult' according to the approximate lengths (<0.8 mm/0.8–1.7 mm/>1.7 mm). This field-classification was based on knowledge of the complete range of body-sizes of this species from laboratory-rearing. To ensure sufficient sample sizes, counts of *E. nivalis* were pooled across five subsequently investigated colonised trees. Relative proportions of the three age-classes were calculated for each sample.

In each exposure zone the amount of each of the epiphyte species was estimated according to their cover: <20%, >20 – <50%, >50%.

### Statistical analysis

Tests were conducted on changes in age-class-compositions in different microhabitat types ( $\chi^2$ -test) and on changes in relative densities of animals in a certain microhabitat when comparing different climatic environments ( $\chi^2$ -tests of goodness of fit, see below). The non-parametric Kolmogorov-Smirnov test was applied when expected frequencies were very small (Lamprecht, 1992). Samples were pooled within each category of the independent variable (Fowler and Cohen, 1986; Mühlenberg, 1989).

The relative density on a given microhabitat '1',  $RD_1$ , expresses the ratio between the absolute density on this microhabitat,  $D_1$ , and the sum of absolute densities on all nine investigated microhabitats (indicated '1'–'9'). Thus, the relative density indicates the relative importance/suitability of '1' for the animals compared with the other microhabitats:

$$RD_1 = \frac{D_1}{\sum_{i=1}^n D_i} \quad (n = 9) \quad (22.1)$$

If the microhabitat '1' was of equal relative importance/suitability during two contrasting climates I and II, the expected relative densities would be equal, to:

$$RD_{e1,I} = RD_{e1,II} \text{ (null hypothesis for the microhabitat '1')}$$

or:

$$\frac{D_{e1,I}}{\sum_{i=1}^n D_{i,I}} = \frac{D_{e1,II}}{\sum_{i=1}^n D_{i,II}} \quad (22.2)$$

Since the density in a microhabitat is calculated as the frequency  $F$  divided by the number of plots, in which this microhabitat was found and investigated (sampling effort  $P$ ), Equation (22.2) can be rewritten as:

$$\frac{F_{e1,I} : P_{1,I}}{\sum_{i=1}^n (F_{i,I} : P_{i,I})} = \frac{F_{e1,II} : P_{1,II}}{\sum_{i=1}^n (F_{i,II} : P_{i,II})} \quad (22.3)$$

This equation allows the calculation of the null expected frequencies on '1' for the climates I and II, standardized for the differences in sampling efforts. Such standardized null expected frequencies were required for the subsequent  $\chi^2$  test of goodness. Four steps were required (E. Glück, H.-J. Krambeck and J. Schimmler, personal communication):

1. Rearrange Equation (22.3) to:

$$\frac{F_{e1,I} : P_{1,I}}{F_{e1,II} : P_{1,II}} = \frac{\sum_{i=1}^n (F_{i,I} : P_{i,I})}{\sum_{i=1}^n (F_{i,II} : P_{i,II})} = \frac{\sum_{i=1}^n D_{i,I}}{\sum_{i=1}^n D_{i,II}} = Z \quad (22.4)$$

2. Replace the expected frequency for '1' during one of the climates by the difference between the other expected frequency and the sum of the two observed frequencies on '1'. This can be done, because the sum of expected frequencies must equal the sum of observed frequencies on a microhabitat:

$$\frac{F_{e1,I} : P_{1,I}}{((F_{1,I} + F_{1,II}) - F_{e1,I}) : P_{1,II}} = Z \quad Z = \frac{\sum_{i=1}^n D_{i,I}}{\sum_{i=1}^n D_{i,II}} \quad (22.5)$$

3. Solve Equation (22.5) for  $F_{e1,I}$ :

$$F_{e1,I} = \frac{Z \times (F_{1,I} + F_{1,II})}{(Z + (P_{1,II} : P_{1,I}))}$$

4. Calculate the second expected frequency as:

$$F_{e1,II} = (F_{1,I} + F_{1,II}) - F_{e1,I}$$

Observed frequencies were tested against the expected frequencies with a  $\chi^2$ -test of goodness of fit applying Yates' correction (Welkowitz *et al.*, 1982).

Comparisons of frequencies during day and night were calculated only on counts for months and areas when night visits were also conducted; data for comparison of weather conditions are from day visits only.

Discriminant analysis was performed using the Systat statistical package (1992).

## RESULTS

### Abundance

The trunks were found to be a suitable macrohabitat for *E. nivalis* throughout the complete period of investigation, but with variable utilization of microhabitats. Densities fluctuated strongly, especially within thalli of *Evernia prunastri* (Figure 22.1). Fluctuations in overall densities on tree trunks was correlated with a higher trunk boundary layer temperature compared to the surrounding air. The only exception was in February when temperatures were extremely low (Figure 22.1). *E. nivalis* was also found on trunks during the rest of the year.

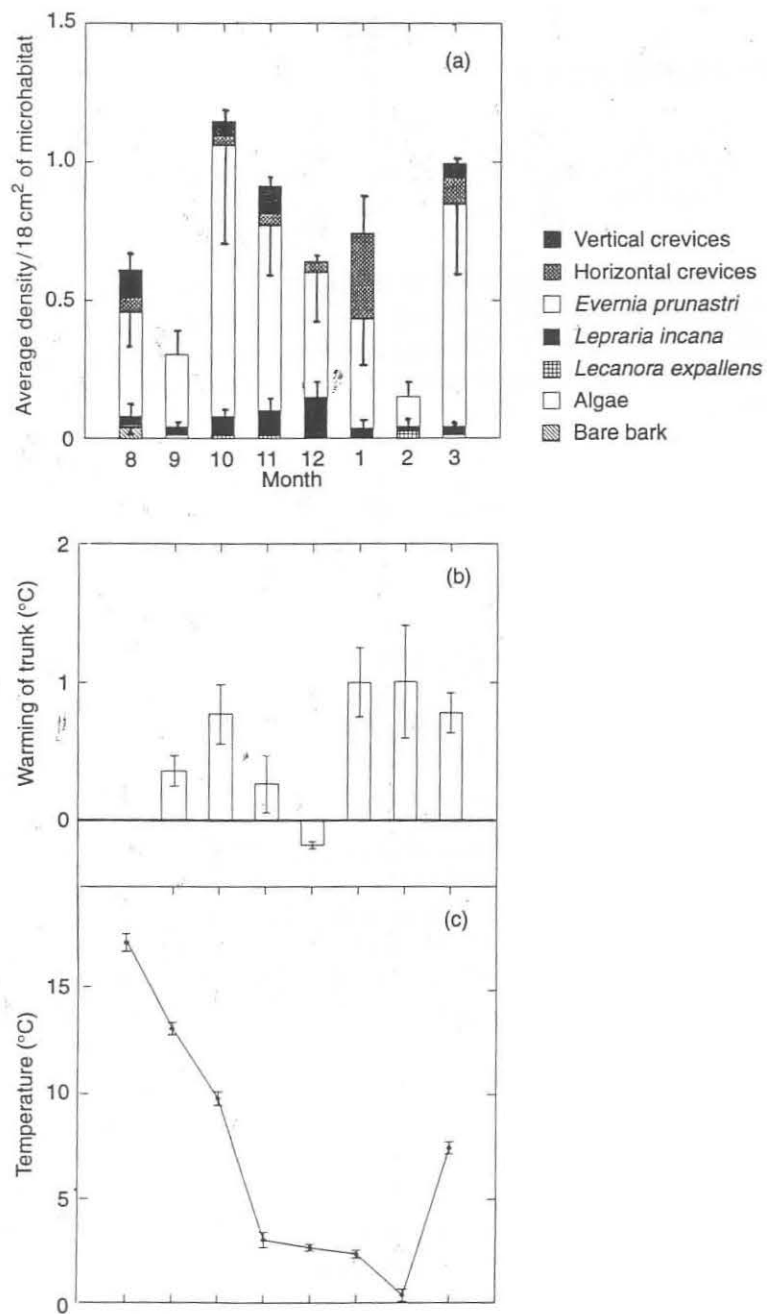


Figure 22.1 (a) Average population densities (± S.E.) of *Entomobrya nivalis* in different types of microhabitats during the investigation period. The area near Rostock (investigated only until September) is not included. (b) Average (± S.E.) differences between temperature of the boundary layer and the free surrounding atmosphere. (c) Average (± S.E.) temperature of the boundary layer.



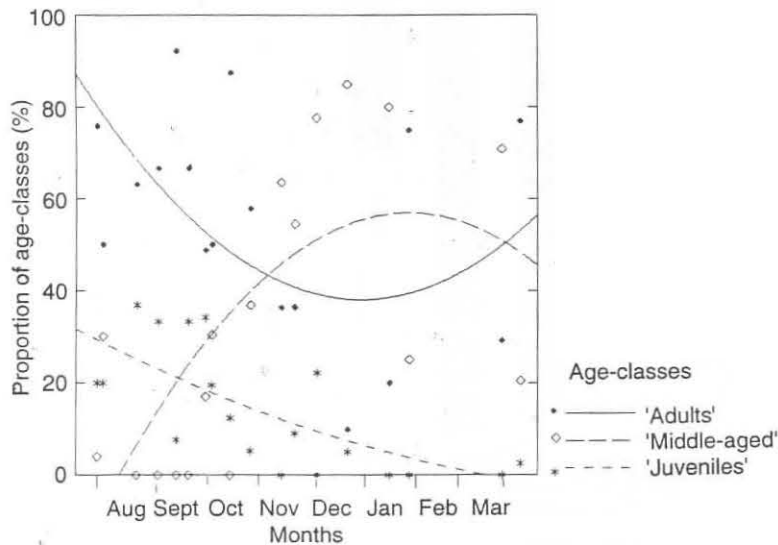


Figure 22.2 Phenology of *E. nivalis* during months of investigation (x-axis), plotted as percentages of different age-classes of *E. nivalis*, curves fitted by quadratic procedure.  $n = 25, 10, 19, 6, 13, 15, 41, 36, 8, 38, 33, 11, 9, 20, 20, 8, 24, 39$  animals per sample, respectively.

#### Phenology and spatiotemporal distribution of age-classes

All age-classes of *E. nivalis* were found on trunks in high numbers and often simultaneously. Life-cycles seemed to be univoltine with hatching mainly in early summer (Figure 22.2). The simultaneously occurring age-classes were segregated in their temporal use of the tree trunks. The abundance of intermediate-aged animals increased significantly during rainy weather, whereas adults were slightly more abundant during sunny weather with <70% cover by clouds ( $\chi^2 = 15.6$  and  $5.76$ ,  $P < 0.001$  and  $< 0.1$ ,  $n = 77$  and  $129$  respectively, d.f. = 2 each). Age-classes also varied in their microhabitat use (for all age classes:  $\chi^2 = 46.11$ , 8 d.f.,  $P < 0.001$ ,  $n = 331$ , Figure 22.3). Frequencies of juvenile animals were proportionally greater on *L. incana* and in vertical crevices ( $\chi^2 = 7.74$  and  $27.04$ ,  $P < 0.05$  and  $< 0.001$ ,  $n = 42$  and  $10$ , respectively, 2 d.f. each). In the latter, animals of intermediate age were completely absent. Adults were very uniformly distributed.

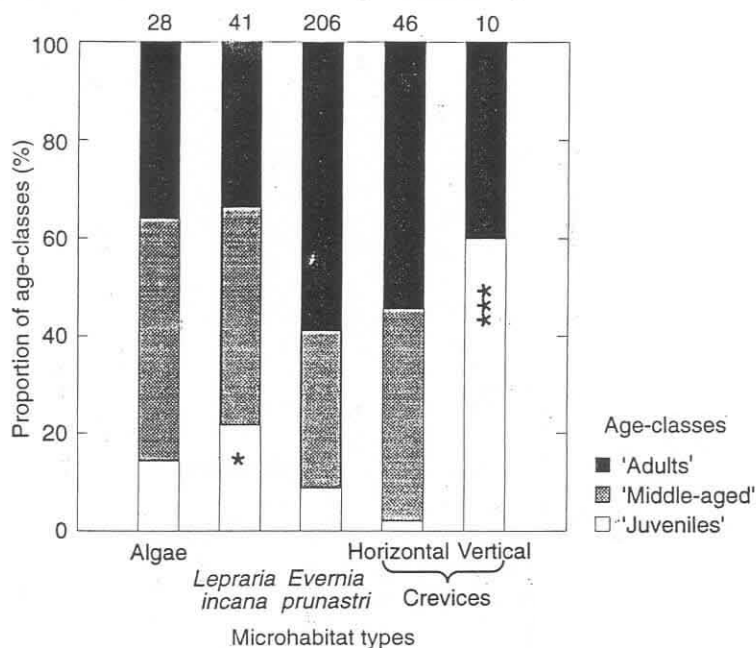


Figure 22.3 Percentage of age-classes in different microhabitats. Sum of animals per habitat-type given on top of each bar. Significantly higher proportional frequencies are stated as \* or \*\*\* ( $P < 0.05$  or  $P < 0.001$  respectively,  $\chi^2$ -test, 2 d.f.). Bare bark and *Lecanora* sp. have been omitted because of low numbers of individuals.

#### Spatial use of microhabitats

Out of nine microhabitat types, four were regularly used by *E. nivalis* (Figure 22.4). Densities were highest in *Evernia prunastri*, followed by the crust-like lichen *Lepraria incana*, horizontal crevices and vertical crevices. Microhabitat use was differentiated according to (i) the basic fruticose or crust-like growth-forms, and (ii) micromorphological characteristics. The avoidance of all crust-like lichens, except *L. incana*, is particularly notable since they are structurally very similar. Bare bark and crusts of algae were also avoided, although the latter was the most common type of microhabitat.

#### Effect of trunk-climate on temporal microhabitat use

##### Univariate analysis

Frequencies on *L. incana*, in *Evernia prunastri* and in horizontal crevices were sufficiently high for statistical analysis of their respective temporal

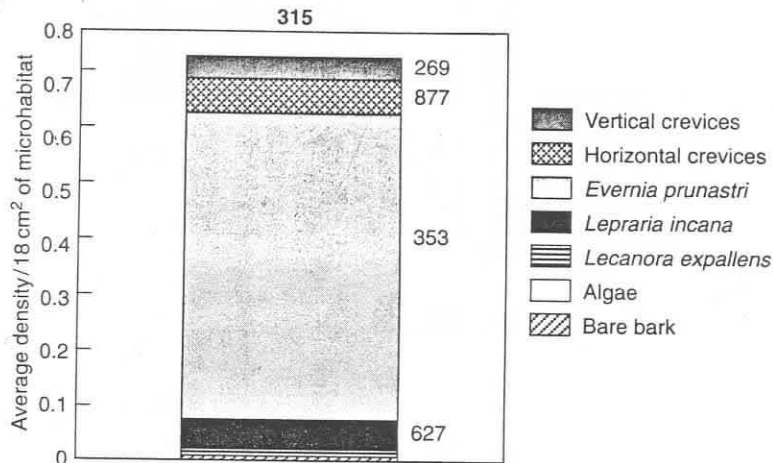


Figure 22.4 Average population densities of *Entomobrya nivalis* on different types of microhabitats. The total number of animals is given in boldface on top of the graph, and numbers of investigated plots of microhabitat types relevant to *E. nivalis* are given to the right of the respective bars. For other microhabitat types the following numbers of plots were investigated: algae, 1060; bare bark, 144; *Lecanora expallens*, 395; *L. conizaeoides*, 42; *Pertusaria albescens*, 138. Note the latter two were not populated at all.

use by *E. nivalis*. Under all climatic conditions considered *Evernia prunastri* was colonized by the largest proportions of *E. nivalis*. On the other hand, *L. incana* and horizontal crevices were used more under certain climatic conditions (Figure 22.5).

*L. incana* was preferred on trunk zones sheltered from wind (Figure 22.5(c)), from radiation (Figure 22.5(a), weather, daytime), from dry or medium humid air or from very high absolute temperatures (Figure 22.5(a)). Furthermore, shelter from high relative temperatures seemed to be required for the use of *L. incana* during strong winds (high convective desiccation), during the day (sun) and above 7°C (Figure 22.5(d)).

Horizontal crevices were preferred in the absence of a waterfilm (Figure 22.5(b)) and under conditions of very low absolute temperatures (Figure 22.5(a)). Furthermore, relatively low temperatures seemed to promote horizontal crevice use below 7°C or during low wind turbulence (high temperature gradient) (Figure 22.5(d)). High correlation of the use of *L. incana* and horizontal crevices with relative temperatures indicates an immense dynamic of *E. nivalis*' distribution, since the corresponding climatic zonation of a trunk quickly changes throughout each day (Nicolai, 1985). On sunny, calm days the respective temperature

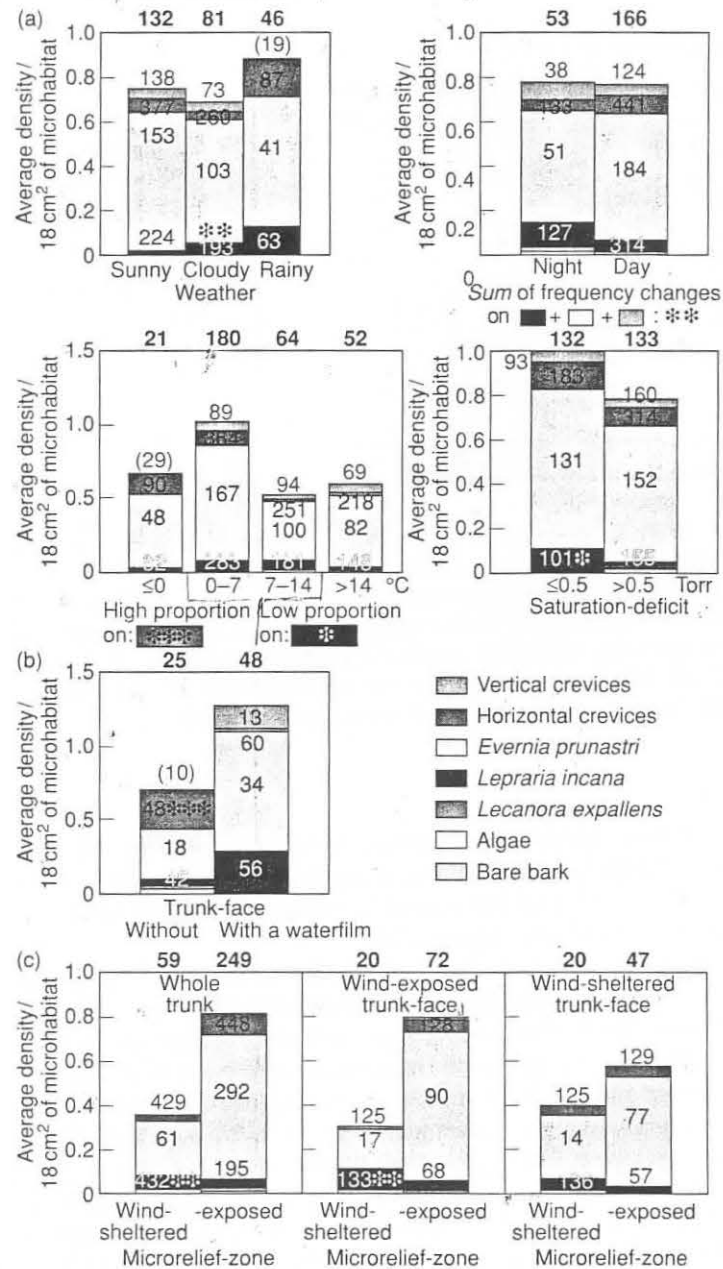
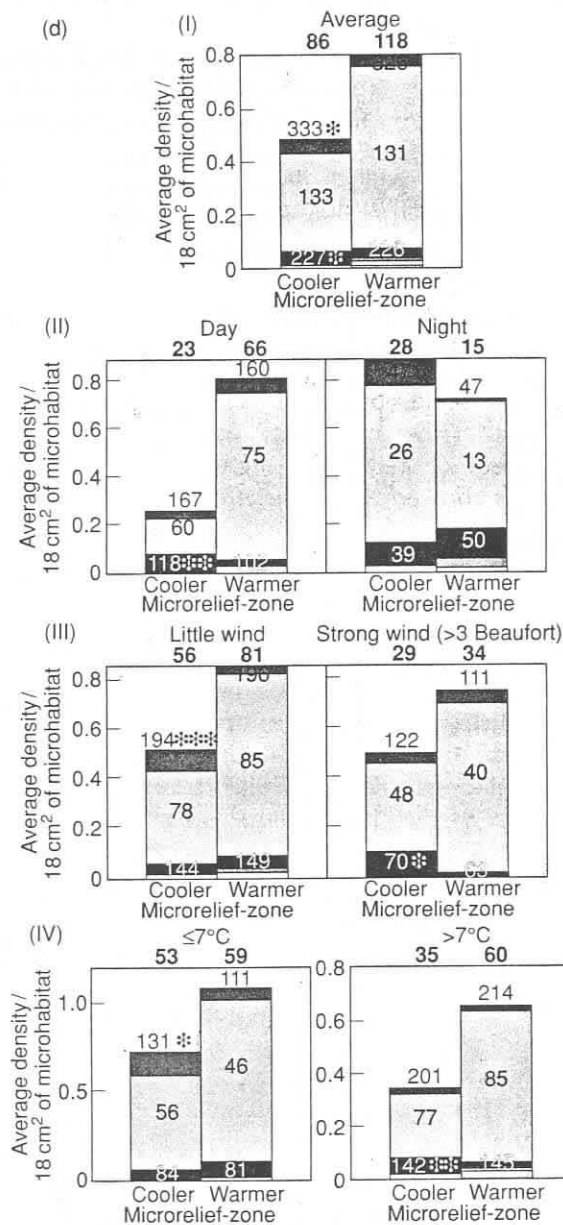
Microhabitat use by *Entomobrya nivalis*

Figure 22.5 Changes in proportions of average densities of *Entomobrya nivalis* on microhabitat types under different climatic conditions: (a) absolute conditions; (b-d) zonation of waterfilm, wind and temperature. Significantly higher proportional frequencies on *L. incana*, in *Evernia prunastri* or in horizontal crevices compared with the neighbouring column are indicated by \*, \*\*



and \*\*\*( $P < 0.05$ ) and  $< 0.001$  respectively, 1 d.f.  $\chi^2$ -test of goodness, except for *L. incana* in Figure 22.5(d) II-IV, where the Kolmogorov-Smirnov test was applied. 'Cloudy' indicates >70% of sky covered by clouds. For details of sample sizes, see Figure 22.4

gradients could reach 20° C and 8°C respectively between opposed trunk faces and microrelief-zones.

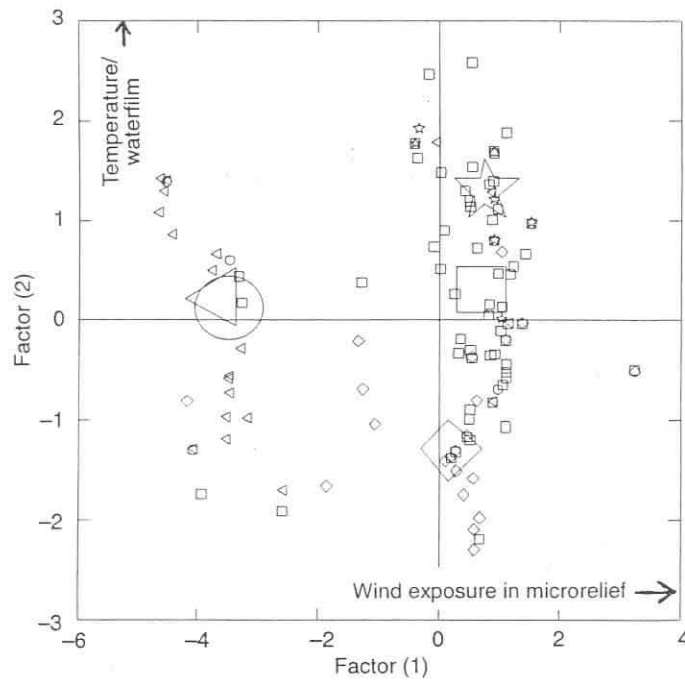
In vertical crevices, animals were found during dry and warm weather conditions (Figure 22.5(a)), but also occurred while the bark was covered with a waterfilm (Figure 22.5(b)). Vertical crevices cannot be differentiated according to the microrelief because they are restricted to layers below bark-ridges. Algae seemed to be used only when sheltered from a waterfilm (Figure 22.5(b)) and from wind by trunk-face and microrelief (Figure 22.5(c)). At night the cooler zones of the microrelief were also used (Figure 22.5(d)).

No significant changes in frequencies were found when solely considering the effect of trunk-face climates. The statistical effects of several independent climatic parameters on *L. incana* use was similar: (i) wind-exposure on the scale of trunk-faces enhanced the effect of wind-exposure within the microrelief; (ii) high absolute temperatures enhanced the effect of relatively high temperatures; and (iii) the day/night changes showed the same effects as sunny/cloudy weather changes during the day.

#### Multivariate analysis

Microhabitat use was predominantly influenced by wind exposure within the microrelief (discriminant analysis factor 1 in Table 22.1) and by temperature and distribution of waterfilms (factor 2). These factors have high canonical correlation scores, indicating high explanatory value. The first factor segregated crust-like microhabitats from those with cavities (Figure 22.6, except of the single animal on *L. expallens* at 0.9,1.7). The latter were further divided by the second factor. Crusts of *L. incana* and algae were, therefore, only used under wind-sheltered conditions and at low or medium temperatures. Horizontal crevices were populated under cold, often wind-exposed conditions without waterfilm. In contrast, use of vertical crevices seemed to be positively correlated with heat and a waterfilm. Use of *Evernia prunastri* was not greatly dependent on any of the factors, as indicated by its position close to (0,0), although usage increased slightly under wind exposure.

The secondary effect of daytime and weather conditions on microhabitat use in multivariate analysis was probably due to the low number of visits at night or during sunny weather. The relative temperature within the microrelief only came into play in correlation with such day/night changes. This confirmed the strong interaction between these factors found in the univariate analysis. Measurements of saturation deficits were not included in the analysis because they were mostly only available for the exposed zones of the bark relief where the sensor could be fixed.



**Figure 22.6** Use of different types of microhabitats according to the climatic variables summarized in the first and second canonical factors of discriminant analysis in Table 22.1. Small symbols indicate animals on algae (○), on *L. incana* (◁), in *Evernia prunastri* (◻), in horizontal (◊) or in vertical crevices (☆). Large symbols indicate respective centroids.

The important first to third canonical factors were each strongly correlated with only one or two different microclimatic variables. This indicates the existence of clear-cut, well-separated climatic influences consisting of only one or a few parameters.

As discussed above, population densities on neighbouring *L. incana* and horizontal crevices were strongly correlated ( $r_s = -0.897$ ,  $P = 0.011$ ,  $n = 17$  zones of exposure colonized by *E. nivalis*), but did not interact significantly with the use of *Evernia prunastri*.

#### Effect of patch size on microhabitat use

The preferred epiphytes *L. incana* and *Evernia prunastri* were highly patchily distributed and often of very low abundance. This did not influence the absolute or relative frequencies of *E. nivalis* on the respective thalli (Figure 22.7).

**Table 22.1** Prevailing factors for microhabitat use according to discriminant analysis presented as significant and independent canonical factors. Numbers indicate correlations with original variables and canonical correlation (last row). The latter indicates the explanatory value of each canonical factor as a degree of its correlation with the original data. Bold numbers indicate correlations of  $> |0.33|$

Original variables	Factors				
	1	2	3	4	5
a) tamabs	-0.02	<b>0.41</b>	-0.04	0.30	0.06
b) dtemp <sub>if</sub>	-0.06	-0.10	-0.20	-0.14	0.01
c) dtemp <sub>mr</sub>	0.02	0.22	-0.10	<b>0.44</b>	0.22
d) I dtemp <sub>if</sub> I	0.14	0.28	-0.15	<b>-0.40</b>	-0.31
e) I dtemp <sub>mr</sub> I	0.05	0.08	0.07	<b>-0.34</b>	-0.32
f) dtemp <sub>atm</sub>	0.09	0.32	-0.27	-0.12	<b>-0.41</b>
g) windsp	-0.03	-0.32	0.27	-0.10	0.33
h) wind <sub>if</sub>	-0.04	0.09	0.06	0.16	0.27
i) wind <sub>mr</sub>	<b>0.77</b>	0.07	0.30	0.03	-0.16
j) sun <sub>if</sub>	0.02	-0.06	-0.21	-0.20	<b>0.42</b>
k) sun <sub>mr</sub>	0.05	0.11	0.05	0.21	0.08
l) wf <sub>if</sub>	-0.18	<b>0.40</b>	<b>0.55</b>	-0.12	-0.14
m) nd	0.20	-0.16	0.11	<b>0.39</b>	-0.26
n) wea	-0.20	0.26	0.03	-0.22	<b>0.40</b>
Canonical correlations:	0.81	0.51	0.31	0.25	0.22

a), absolute temperature; b)/c), difference in temperature between opposing trunk-faces/microrelief-zones; d)/e), strength of temperature gradient (= 0 or 1 when  $|b|/|c| < \text{or} > 1$ ); f), warming of boundary layer compared with surrounding atmosphere; g), wind speed (Beaufort scale); h)/i), wind-exposure of the trunk-face/microrelief-zone (+1/-1); j)/k), sun-exposure of the trunk-face/microrelief zone; l), trunk-face without/with waterfilm during precipitation (+1/-1); m), night/day (0/1); n), sunny/cloudy/rainy weather (1/2/3)

### Effect of optical-searching method

Animals were not significantly chased away from exposed crusts into hide-outs by searching with a hand-lens. Altogether 36 animals were found on surfaces of crusts with the hand-lens (with 18-cm<sup>2</sup> plots). On plots where no animals were found in this way, the previous counts with a distance-lens (from a distance of 40 cm) on much larger plots of 31 cm<sup>2</sup> revealed only 11 additional animals. Moreover, animals that were spotted with the distance-lens were often 'tested' by approaching them with a hand-lens. This did not induce 'flight' behaviour.



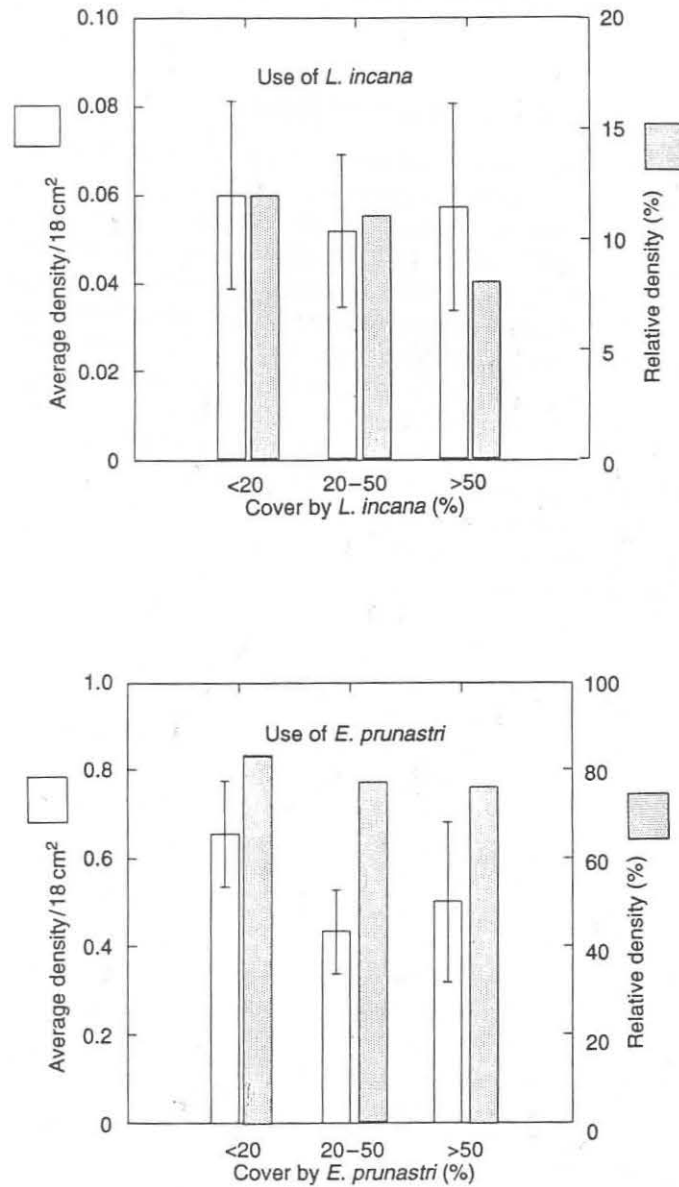


Figure 22.7 Densities of *Entomobyra nivalis* on thalli of *L. incana* and of *Evernia prunastri* covering small, medium or large parts of the trunk's respective zone of exposure. Absolute densities ( $\pm$  S.E.), relative density = (average density of *E. nivalis* on the respective lichen species) : (sum of average densities on all microhabitat types). Habitat use does not switch significantly with changing densities of the epiphyte.

## DISCUSSION

## Causes and functions of distributional patterns

Exposed trunks appear to be a habitat for *E. nivalis* throughout the year. Colonization of tree trunks may confer an energetic benefit for the animal as these vertical, dark structures can act as 'solar-panels', especially during winter (Nicolai, 1985). Indeed, densities on all microhabitat-combined correlated strongly with the warming of the bark boundary layer, except in February when average temperatures were near 0°C. Such 'thermophilic' behaviour of colonization corresponds well to the preference of *E. nivalis* for high temperatures in the laboratory (17–27°C depending on growth stage; Müller-Kraenner, 1990).

Alternatively, high air humidity and night conditions have been suggested as possible prevailing stimuli for the colonization of trunks by Collembola (Bowden *et al.*, 1976; Bauer, 1979). However, these factors appear to rarely correlate with the density of *E. nivalis* (Figure 22.5(a)). Furthermore, at night and at high air humidity the boundary layers of trunks have the same or even lower temperatures than the surrounding atmosphere (Nicolai, 1985; A. Prinzing, unpublished data). Night conditions and air humidity, therefore, do not explain the strong month-to-month fluctuations in abundance.

On solitary, exposed trunks this beneficial warming of the boundary layer is strongest due to the direct exposure to the sun (Nicolai, 1985). This might compensate for the higher risk of desiccation as well as drowning compared with much more sheltered trunks in forests. In fact, *E. nivalis* was found on the solitary trunks about as often as it was to be found on sheltered trees (von Allmen and Zettel, 1982; André, 1983; Büchs, 1988; Müller-Kraenner, 1990).

Tree trunks are utilized throughout the year, while positions within the mosaic of microhabitats changed. Where this microhabitat mosaic is absent, tree trunks are only colonized temporally after rain or at night on the algae-covered trunks of ashes and legs of traps investigated by Bowden *et al.* (1976) as well as the smooth algae-covered beeches in Bauer (1979). Hence, trunks are energetically favourable macrohabitats throughout the year, as long as a variety of microhabitats is available.

In this study population density collapsed several times, followed by rapid recolonization. Recolonization in autumn and winter cannot be caused by new generations of individuals because development is univoltine. Instead, only the immigration of animals from the soil or from upper parts of the tree can account for population recovery. Such immigration would also explain the short-term increase in the density of adults during sunny weather and, to a greater extent, those of middle-aged individuals in rainy weather. Immigration of middle-aged

individuals also explains the increase in total population density of *E. nivalis* under rainy as compared with cloudy weather. Therefore, middle-aged animals are capable of connecting corticolous populations to those in other habitats and of colonizing depleted trunk microhabitats.

The complementary increase in middle-aged and adult stages during rainy and sunny weather, respectively, corresponds well with the comparatively lower temperature- and higher air-humidity preferences of middle-aged animals in the laboratory (Müller-Kraenner, 1990). Juveniles, however – being much more sensitive to environmental conditions – tend to be constant in their use of the trunk. For juveniles, migration may be energetically too costly, or the risk of desiccation or drowning may be too great when crossing unsheltered microhabitats. Similarly, on subalpine spruce trees juvenile animals do not migrate onto trunks above 3–4 m (von Allmen and Zettel, 1982). Besides the preferences in the laboratory, the microhabitat use of middle-aged animals in the field also corresponds to their large-scale migrations: these animals use horizontal crevices comparatively more than did other stages. Since these crevices are extremely common and interconnected to each other, this stage is able to rely on the dense network of sheltered microhabitats during migration.

All age-classes were found in large numbers in this study and often coexist on the same trunk, despite their very different sensitivities (Müller-Kraenner, 1990). Among these age-classes, middle-aged and adult animals segregate temporally on a macrohabitat scale, as discussed above. On the other hand, segregation of juveniles was detected on a microhabitat scale: the complete protection from sunny and windy weather conditions provided by vertical crevices is probably most important for juveniles, because juveniles (1) have the highest humidity- and lowest temperature-preferences (Müller-Kraenner, 1990), and (2) are not capable of compensatory large-scale migrations to adjacent macrohabitats as are other stages. Only middle-aged animals are found to be absent from vertical crevices, perhaps because these crevices are of no value during the preferred rainy weather conditions. High proportions of juveniles also are found on *L. incana*, followed by middle-aged animals. This corresponds to the high palatability of such extraordinarily soft thalli for animals with mouthparts as minute as those in young Collembola. These animals are often observed to graze upon *L. incana*.

Such spatiotemporal patterns permit a physiologically optimized use of microhabitats and avoid competition between age classes. They may also spread the risks of this unpredictable climatic environment among animals of very different physiological sensitivities and spatiotemporal habitat use. An alternative phenological strategy to cope with such extreme and unpredictable climates would be a very rapid life-cycle (Tischler, 1990).

The fruticose lichen *Evernia prunastri* is used ubiquitously and it seems that *E. nivalis* always find sufficient climatic shelter as well as food here. Within the thalli suitable shelter and food are always restricted to certain regions and these shift according to the climate, leading to microscale migrations of *E. nivalis* within thalli (Prinzing and Wirtz, 1997, Chapter 23, this volume). In contrast, microhabitats other than *Evernia prunastri* are used more under certain climatic conditions. This might be explained by the physiological suitability of the microhabitats for animals. Indications of such functions can be derived from the temporal use of microhabitats, taking into account: (i) their observed properties; and (ii) the insects' physiological needs (Prinzing and Wirtz, 1997, Chapter 23, this volume). *L. incana* has an unusually hydrophobic surface and this protects insects from drowning in a waterfilm. Indeed, *L. incana* was heavily utilized even on water-covered trunk-faces. In addition, *L. incana* has a soft, palatable thallus, even when dry and may be highly populated for nutritional reasons. *L. incana* is not used when exposed to dry air, direct radiation, high relative or absolute temperatures and convection and may not offer shelter from such risks of desiccation due to its crust-like growth-form.

The highly favourable conditions in *Evernia prunastri* and on *L. incana* probably also reduce the chance of insects switching to other cryptogam species when these lichens are very rare. This contrasts to the classic behaviour of herbivores on phanerogams (Crawley, 1983).

Crusts of *Pertusaria albescens* were not used at all, even though when the cortex layer was absent, they were hydrophobic and soft like *L. incana*. However, *P. albescens* has much higher concentrations of lichen acids in its medulla layer (Culberson, 1969), and these are known to reduce grazing (Stahl, 1904; Lawrey, 1980). Algal crusts only become soft, and thus readily palatable, above about 90% air humidity and during rain these algae quickly cover with a waterfilm. Correspondingly, *E. nivalis* was only found on algae when strongly sheltered from convective desiccation as well as from a waterfilm. If this characterization of algae as a microhabitat is true, Collembola would be forced to abandon tree trunks that are exclusively covered by algae during adverse weather conditions, as found by Bowden *et al.* (1976) and Bauer (1979).

In contrast to *L. incana* and algae, horizontal crevices seemed to offer sufficient shelter from desiccation due to wind and radiation. Correspondingly, in laboratory experiments cavity-microhabitats (dry thalli of *Evernia prunastri*) strongly increase the tolerance of corticolous microarthropods to desiccation as compared to a flat substrate (single branches of *Evernia prunastri*; Prinzing and Wirtz, 1997, Chapter 23, this volume). Horizontal crevices are also used more below 0°C. Here the crevices are free of hoarfrost or snow that otherwise often cover the trunk's surface, making food inaccessible in other microhabitats. These

results confirm similar anecdotal winter observations made by Agrell (1941) and von Allmen and Zettel (1982). Horizontal crevices do not offer shelter from a waterfilm and are then avoided. They also offer very few algae or lichens as a food source and are correspondingly avoided when not needed for shelter. Thus the flexible and occasional use of horizontal crevices and *L. incana* enable *E. nivalis* to compensate for the extreme and changeable climates on exposed tree trunks.

Patterns of microhabitat use also may be determined at least in part by factors other than the physiological advantages presented above (e.g. natural enemies, competitors or different birthrates). However, the size of habitat patches of *L. incana* and horizontal crevices are small and their quality for the animals changes quickly compared with the larger range and longer lifespan of the individual animals. Thus, only an immediate response of each single animal to the momentary climatic and nutritional conditions in a habitat patch would result in the observed fine grained patterns of spatiotemporal habitat use (Schindler, 1988). On *Evernia prunastri* the spatiotemporal structure of the environment is different for *E. nivalis*: complete thalli do not change in suitability in the short term and most animals do not seem to leave the thalli when climatic conditions change. This is confirmed by the artificial wetting of bark and *Evernia prunastri* (Prinzing and Wirtz, 1997, Chapter 23, this volume). Animals stay in *Evernia prunastri* thalli but leave the bark crevices and move around for distances of tens of centimetres on the bark-surface. Furthermore, in *Evernia prunastri* the population densities are comparatively high. Under these conditions the effects of competition and natural enemies become more important (Schindler, 1988). *Evernia prunastri* is also preferred by most of *E. nivalis*' potential corticolous competitors (Entomobryidae, Psocoptera and Oribatei), predators (spiders, mainly *Lathys humilis* and *Entelecara penicillata*) and entomophagous fungi (mainly *Trichoderma viride* and *Beauveria bassiana*) (Prinzing and Wirtz, 1997, Chapter 23, this volume; A. Prinzing, unpublished data). In rare cases the thalli of *Evernia prunastri* are also obviously overgrazed (Laundon, 1971; Prinzing, 1997). Hence, long-term changes in *E. nivalis*' population density on *Evernia prunastri* may be due to competition and/or predation effects at the population and community levels. This evidence suggests that the spatiotemporal suitability of the microhabitats strongly influences the type of population regulation acting upon *E. nivalis* and the type of community interactions which subsequently develop.

#### Conclusions on microhabitat use: prerequisites and significance

Generally, the small patches of microhabitats present offer only enough food and favourable climatic conditions within the sheltered atmospheric

boundary layer for minute organisms. Furthermore, only eurytopic species are able to show such a flexible use of microhabitats, including habitat changes on very different spatial scales: between different zones within a thallus of *Evernia prunastri*, between horizontal crevices and *L. incana*, and between the trunk and neighbouring habitats. Therefore, minute size and eurytopy might be prerequisites, rather than disadvantages for coping with extreme trunk environments. These characters permit the colonization of tree trunks through the extremely differentiated, flexible, accurate and adaptable use of microhabitats. Thus, sensitive Collembola can utilize the mosaic pattern of microhabitats on exposed tree trunks despite the generally extreme climate. The importance of this strategy is confirmed by the dominance of eurytopic microarthropods as grazers (Nicolai, 1985; Büchs, 1988; Prinzing and Wirtz, 1997, Chapter 23, this volume). The colonization of the canopy layer by non-flying arthropods might have been ontogenetically or phylogenetically preceeded by such eurytopic, small-scale stages on trunks.

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